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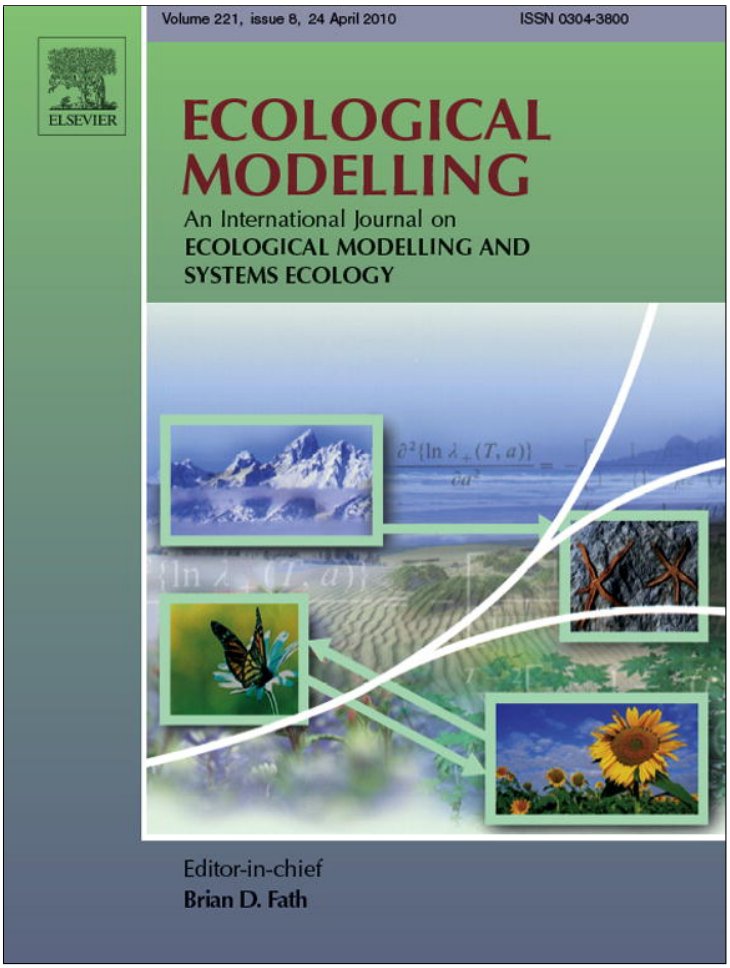

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Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia

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ABSTRACT

The quality of climate models has largely been overlooked as a possible source of uncertainty that may affect the outcomes of species distribution models, especially in the tropics, where comparatively few climatic stations are available. We compared the geographical discrepancies and potential conservation implications of using two different climate models (Saga and Worldclim) in combination with the species modelling approach Maxent in Bolivia. We estimated ranges of selected bird and fern species biogeographically restricted to either humid montane forest of the northern Bolivian Andes or seasonal dry tropical forests (in the Andes and southern lowlands). Saga and Worldclim predicted roughly similar climate patterns of temperature that were significantly correlated. Precipitation layers of both climate models were also roughly similar, but showed important differences. Species ranges estimated with Worldclim and Saga likewise produced different results. Ranges of species endemic to humid montane forests estimated with Saga had higher AUC (Area under the curve) values than those estimated with Worldclim, which for example predicted the occurrence of humid montane forest bird species near Lake Titicaca, an area that is clearly unsuitable for these species. Likewise, Worldclim overpredicted the occurrence of fern and bird species in the lowlands of the Chapare region and well south of the Andean Elbow, where more seasonal biomes occur. By contrast, Saga predictions were coherent with the known distribution of humid montane forests in the northern Bolivian Andes. Estimated ranges of species endemic to seasonal dry tropical forests predicted with Saga and Worldclim were not statistically different in most cases. However, detailed comparisons revealed that Saga was able to distinguish fragments of seasonal dry tropical forests in rain-shadow valleys of the northern Bolivian Andes, whereas Worldclim was not. These differences highlight the neglected influence of climate layers on modelling results and the importance of using the most accurate climate data available when modelling species distributions.
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1. Introduction

Species distribution models (SDM) are probably one of the most promising tools biogeographers have to improve the understanding of biodiversity patterns and their relationship with climate and topography (Cumming, 2000; Bahn and McGill, 2007). The use of modelling techniques implies predicting the distribution of species, and therefore, these techniques inherently have some level of uncertainty that researchers must consider. Discordant predictions rendered by different modelling techniques using the same data have revealed different levels of uncertainty (Elith et al., 2006). One of the most relevant outcomes comparing different species distribution models is that presence–absence models offer more accurate estimates than presence-only models (Elith et al., 2006). However, presence–absence models are of limited applicability especially in the tropics, where low densities of study sites prevent their use (Anderson et al., 2003).

The species distribution model chosen, however, is not the only source of uncertainty (Araújo and New, 2007). Other sources include the spatial structure of the field data that may be collinear

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with environmental variables (Araújo and Guisan, 2006; Loiselle et al., 2008). For example, most of the species presence records come from localities that are easily accessible and that are clustered in areas near the centre of the range of climatic conditions under which a species occurs (Loiselle et al., 2008). Hence, records often do not cover the complete range of environmental variability that a species of interest inhabits. The number of available records also has an inverse impact on the quality of the prediction (Araújo et al., 2005; Soria-Auza and Kessler, 2008). Pöyry et al. (2008) showed that inherent behavioural and mobility characteristics of the species under study may also have an effect on the predictive power of species distribution models. Additionally, Araújo and Guisan (2006) found that models tend to predict the distribution of range-restricted species better than those of widespread species. Moreover, the choice of environmental variables used to model species distributions may result in different distribution maps for the same species (Luoto et al., 2007).

One of the least studied sources of uncertainty in species distribution modelling comes from the environmental data used to run the models, particularly the climate data. Climatic data used to model species distributions are raster-layers that result from extra- and interpolating data collected from climatic field stations (hereafter called field stations). Therefore, different spatial patterns may arise for a given environmental variable depending on the extra- or interpolation procedures used. Temperate regions have several climate models constructed from very robust networks of field stations, whereas tropical countries lack such robust systems. Notwithstanding this limitation, considerable advances in constructing reliable climatic layers at a global scale have been made in the last few years. Worldclim (Hijmans et al., 2005) is perhaps the most outstanding global climate data set. It was reported to accurately represent climate in North America and Europe (Hijmans et al., 2005), and consequently has been used repeatedly used in a wide range of biogeographic studies, including testing the potential effects of climate change on species ranges (Araújo and Rahbek, 2006; Graham et al., 2006; Hernandez et al., 2008). However, the accuracy of the model in tropical areas remains to be evaluated, although Killeen et al. (2007) have pointed out flaws of Worldclim, as for example an artificial ovoid-shaped centre of high precipitation for the central Bolivian lowlands.

In the present study we aim to highlight the geographical discrepancies of using two different climate data sets to estimate patterns of species richness of a set of bird and fern species characteristic of humid montane and seasonally dry tropical forests in Bolivia. The climate data sets used were Worldclim and the alternative model Saga (hereafter called climate models). Saga has been used for climate models in Europe (Böhner, 2005) and Bolivia (Kessler et al., 2007), whereas Worldclim has a global coverage (Hijmans et al., 2005). Although both climate models use the same raw data to produce environmental raster-layers, they apply distinct mathematical processes to construct the models. To assess the impact of climate model choice on species distribution models, we first compared the predictions of the two climate models. Then we used the species distribution model Maxent (Phillips et al., 2006; Phillips and Dudík, 2008), in combination with each climate model, to model the ranges of the selected species and compared the resulting species range maps.

2. Methods

2.1. Study area and species data

Bolivia covers slightly more than one million square kilometres in south-central South America, with about one-third of the country in the Andes and the remainder in the lowlands. Humid montane forests range from approximately 500 m to ca. 4000 m. This type of forest is the dominant vegetation on the east Andean slopes northwest of the Andean Elbow (ca. 18°S) (green polygon; Fig. 1a). Humid montane forests are considered one of the most diverse ecoregions in Bolivia with high levels of endemism (Ibisch et al., 2003; Kessler, 2002a,b; Herzog et al., 2005; Soria-Auza and Kessler, 2007). South of the Andean Elbow, humid montane forests have a more patchy distribution, forming habitat islands in a matrix of seasonally dry tropical forest. The north-westernmost distribution of seasonally dry tropical forests reaches the central Andean region of La Paz department. At this latitude seasonally dry tropical forests are fragmented and surrounded by either other high Andean vegetation types (puna grasslands) or humid montane forests (Herzog and Kessler, 2002, 2006; Ibisch and Mérida, 2003; Wood, 2006; Linares-Palomino and Kessler, 2009) (orange polygon; Fig. 1a). Seasonally dry tropical forests are the dominant vegetation in the subtropical lowlands of southern Bolivia, where several types of dry vegetations are commonly recognized (Chaco, Cerrado and Chiquitano dry forests) (Herzog and Kessler, 2002; Ibisch and Mérida, 2003) (Fig. 1a). Tropical rain forests, on the other hand, occur in northern Bolivia and extend along the eastern base of the Andes south to about 18°, forming a thin band limited to the east by the seasonally flooded grasslands of Beni (in central Bolivia).

For species distributional data, we used the database of Bolivian pteridophytes compiled by M. Kessler and A.R. Smith (Soria-Auza and Kessler, 2008), and the distributional database of birds of Bolivia of Asociación Armonia–BirdLife International (Hernandez et al., 2008). For the present study, 23 bird and 22 fern species were selected according to two criteria: (1) they are characteristic of either humid montane forests north of the Andean Elbow or of seasonally dry tropical forests, (2) they have at least 15 geographically independent records, and a relative good level of knowledge of their distribution. In total, we had 1840 locality records for all species combined, with an average of 38.3 ± 16.7 records per species. The number of records per species varied from 15 (*Myiopsitta monachus*) to 81 (*Polioptila dumicola*).

The subset of fern species characteristic of humid montane forests included six species of the genus *Cyathea* (tree-ferns) that are tightly associated with humid montane forests. Although *Cyathea* species are not categorized as threatened, they are the only group of ferns experiencing direct human impact on their populations as their "trunks" are harvested to make flower pots. Of the 14 bird species characteristic of this habitat one is endemic to Bolivia (*Grallaria erythrotis*).

The subset of species characteristic of the seasonally dry tropical forests was comprised of 15 and 12 species of ferns and birds, respectively. From this group of species, the Bolivian endemic *Cranioleuca henricae* is listed as endangered under IUCN Red List criteria. *Tarphonomus harterti* is endemic to the country. The complete list of species is detailed in Table 1.

2.2. Selection of environmental variables and climate models

We used precipitation and temperature variables that describe the general pattern and annual variability of the climate estimated by both climate models at a resolution of 30 arc s. Variables included (1) annual precipitation, (2) mean precipitation during the three driest months, (3) mean precipitation during the three wettest months, (4) annual precipitation range (precipitation of the wettest month minus precipitation of the driest month), (5) mean annual temperature, (6) mean temperature during the three hottest months, and (7) mean temperature during the three coldest months. Because some of these environmental variables may be collinear, we checked for collinearity following the approach described by Blanchet et al. (2009). We entered the variables one by one into a matrix and then computed at each step the determinant

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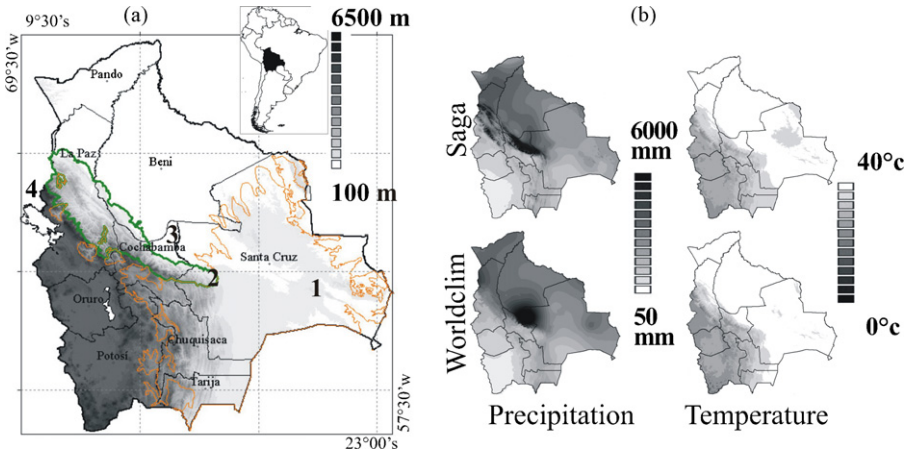

Fig. 1. (a) The study area detailing the administrative division of Bolivia and the digital elevational model of Bolivia in the background. Numbers represent localities mentioned in the text: (1) Serranía de Santiago, (2) Andean Elbow, (3) the Chapare region, (4) Lake Titicaca. The green polygon shows the distribution of continuous humid montane forests, orange polygons the distribution of the seasonally dry tropical forests. (b) Climatic layers of mean annual precipitation (left) and temperature (right) predicted by the Saga (top) and Worldclim (bottom) models. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of the article.)

of its correlation matrix. Variables are completely collinear when the determinant's value equals zero. After this process we eliminated annual precipitation range and mean precipitation during the wettest month.

Worldclim (Hijmans et al., 2005) is a comprehensive climate data set that covers most of the Earth's surface at a resolution of 30 arc s. Worldclim was compiled from available meteorological station networks. The authors used the thin-plate splines smoothing procedure available in ANUSPLIN 4.3, as described by Hutchinson (1995). A second-order spline was fitted using latitude, longitude and elevation as independent variables because this produced the lowest overall error (see Hijmans et al., 2005 for more details). This technique has been used in several global studies, and performed relatively well in comparative tests of multiple interpolation techniques (New et al., 1999, 2002).

Whereas the Worldclim approach is an interpolation technique rather than a modelling approach, the estimation of climate variables via Saga uses an empirical modelling scheme. Saga integrates statistical downscaling and terrain parameterization methods to enable the physically consistent estimation of climate layers. The statistical downscaling consists of linking data collected from meteorological stations to large-scale circulation patterns. Since spatio-temporal climate variations in mountainous environments are also significantly controlled by regional to local scale topography and other processes, digital elevation model (DEM) derived terrain parameters are integrated in order to increase the predictive power and the empirical congruence of the spatial transfer functions. The required data for this modelling process consist of circulation variables either derived from general circulation models (GCM) or from retroactively modelled atmospheric fields, a high resolution digital elevation model (DEM) and available time series data from meteorological station networks. A more comprehensive description of this modelling approach and its limitations is given in Böhner (2005).

2.3. Comparison of climate models

We randomly plotted 1000 points over the surface of Bolivia. In order to prevent pseudo-replication (more than a point from a single grid), points were a least 1 km apart from each other (the resolution of the climatic layers from Saga and Worldclim). Then we imported this georeferenced file into DIVA GIS 5.4. The corresponding environmental variables of each point were extracted from both climate models. We used SAM 3.0 to correlate the correspondent environmental variables from both climate models (e.g. mean annual temperature from Worldclim vs. that from Saga). We used the adjusted p values following Dutilleui' (1993) correction to account for the effect of spatial autocorrelation.

2.4. Modelling species distribution

We used Maxent (Maximum Entropy) to model species distributions (Phillips et al., 2006; Phillips and Dudík, 2008). This method has been reported to outperform other presence-only methods (Elith et al., 2006), even with limited amounts of occurrence data (Pearson et al., 2007). Auto features were maintained to find out the best relationship between species occurrence data and environmental variables, and settings were set to remove duplicate presence records at the resolution of the environmental layers.

Prior to modelling, we randomly partitioned the occurrence data of each species into two subsets. Seventy-five percent of the records were used to model species distributions (training data), and 25% to evaluate the model (testing data). We repeated this procedure 20 times per species. The partition was performed randomly each time following a bootstrapping procedure. We therefore modelled 20 versions of each species' distribution (hereafter termed versions). In order to compare the modelled species distributions, and consequently, the estimated pattern of species richness by both climate models, we converted the probability values given by Maxent into presence–absence values using the maximisation of sensitivity and specificity values as threshold (Canran et al., 2005). The final ranges of each species included only the grid cells predicted to potentially contain the species in all 20 versions. We used the area under the curve (AUC) to evaluate the general accuracy of every version modelled. This measure has been recommended for evaluating predicted species distributions because it avoids the supposed subjectivity of threshold-selection when continuous probability derived scores are converted into binary presence–absence (Fielding and Bell, 1997).

Wilcoxon tests were used to test for differences between AUC values produced by the modelled estimations from Saga and Worldclim at the species level and between species. At the species level, each AUC value of a modelled version was considered a repetition, so we had 20 repetitions. At the between-species approach the averaged values of AUC per species were considered repetitions. Finally, we also compared the differences in the predicted patterns of species richness estimated by each climate model. We created a map of disagreement between both maps of species richness

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Table 1
Comparison between versions (intraspecific comparisons) and final maps constructed with Maxent using Saga and Worldclim data layers. Each row shows the average and standard deviation of AUC values based on 20 Maxent runs, followed by *z* value (of the Wilcoxon test) and the corresponding *p* values. Bold values indicate significant differences, highlighting the higher values.

Species	Taxa	Saga		Worldclim		Wilcoxon test	
		AUC	±SD	AUC	±SD	*z*	*p* value
Humid montane forests							
Andigena cucullata	Bird	**0.98**	0.001	0.94	0.002	4.78	0.00
Atlapetes rufinucha	Bird	**0.95**	0.001	0.88	0.001	4.70	0.00
Conirostrum ferrugineiventre	Bird	**0.96**	0.001	0.88	0.001	4.40	0.00
Cranioleuca albiceps	Bird	**0.95**	0.001	0.89	0.001	4.70	0.00
Cyanolyca viridicyanus	Bird	**0.93**	0.001	0.89	0.001	4.57	0.00
Cyathea austropallescens	Fern	**0.97**	0.001	0.91	0.001	2.88	0.00
Cyathea delgadii	Fern	**0.98**	0.015	0.92	0.003	4.17	0.00
Cyathea multiflora	Fern	**0.98**	0.003	0.91	0.003	3.34	0.00
Cyathea pungens	Fern	**0.96**	0.004	0.86	0.005	3.61	0.00
Cyathea squamipes	Fern	0.92	0.002	**0.94**	0.002	3.74	0.00
Cyathea subincisa	Fern	**0.94**	0.001	0.86	0.001	4.34	0.00
Delothraupis castaneoventris	Bird	**0.95**	0.001	0.88	0.001	4.62	0.00
Entomodestes leucotis	Bird	**0.95**	0.001	0.88	0.003	4.78	0.00
Eubucco versicolor	Bird	**0.99**	0.002	0.89	0.002	4.72	0.00
Grallaria erythrotis	Bird	**0.96**	0.001	0.89	0.001	4.78	0.00
Metallura aeneocauda	Bird	**0.96**	0.001	0.86	0.001	4.70	0.00
Myiornis albiventris	Bird	**0.95**	0.002	0.86	0.001	3.70	0.00
Psarocolius atrovirens	Bird	**0.96**	0.001	0.90	0.002	4.78	0.00
Scytalopus parvirostris	Bird	**0.98**	0.002	0.90	0.001	4.30	0.00
Zimmerius bolivianus	Bird	**0.96**	0.002	0.87	0.002	3.87	0.00
Subset of species		**0.96**	0.018	0.89	0.024	3.27	0.00
Seasonally dry tropical forests							
Adiantum rufopunctatum	Fern	0.89	0.003	0.89	0.001	1.89	0.06
Adiantopsis chlorophylla	Fern	0.93	0.025	0.92	0.026	1.38	0.17
Anemia australis	Fern	0.87	0.006	0.86	0.006	0.05	0.96
Anemia herzogii	Fern	0.87	0.014	0.88	0.013	0.25	0.80
Anemia ferruginea	Fern	0.93	0.014	0.92	0.013	2.19	0.08
Anemia myriophylla	Fern	0.91	0.006	0.91	0.010	0.76	0.44
Anemia tomentosa	Fern	0.88	0.007	0.88	0.005	0.05	0.96
Argyrochosma flava	Fern	0.88	0.010	0.88	0.009	1.17	0.24
Arremon flavirostris	Bird	**0.93**	0.002	0.89	0.003	4.63	0.00
Asplenium inaequilaterale	Fern	0.87	0.059	0.87	0.058	2.09	0.04
Asplenium lorentzii	Fern	0.91	0.002	0.91	0.004	1.48	0.14
Astrolepis sinuata	Fern	0.93	0.052	0.92	0.007	0.87	0.39
Cranioleuca henricae	Bird	0.98	0.021	0.98	0.021	0.87	0.39
Doryopteris lorentzii	Fern	0.94	0.025	0.93	0.010	0.15	0.88
Doryopteris raddiana	Fern	0.94	0.017	0.94	0.015	1.07	0.28
Formicivora melanogaster	Bird	0.93	0.006	**0.95**	0.005	4.17	0.00
Myiopsitta monachus	Bird	0.97	0.003	0.97	0.002	1.66	0.10
Nystalus maculatus	Bird	0.96	0.003	0.96	0.004	1.50	0.13
Pecluma filicula	Fern	0.90	0.003	0.90	0.004	0.20	0.84
Polioptila dumicola	Bird	0.95	0.006	0.94	0.006	1.22	0.22
Poospiza boliviana	Bird	0.92	0.002	0.92	0.001	1.25	0.21
Selaginella sellowii	Fern	0.90	0.005	0.90	0.005	1.78	0.07
Serpophaga munda	Bird	0.89	0.004	**0.92**	0.002	4.17	0.00
Stigmatura budytoides	Bird	0.94	0.002	**0.96**	0.002	3.96	0.00
Suiriri suiriri	Bird	**0.97**	0.005	0.90	0.009	3.11	0.00
Synallaxis scutata	Bird	0.90	0.002	0.90	0.004	2.58	0.01
Tarphonomus harterti	Bird	0.88	0.012	**0.90**	0.033	4.78	0.00
Subset of species		0.92	0.033	0.92	0.031	2.02	0.18
All species		0.94	0.034	0.90	0.030	2.02	0.04

by performing a cell-to-cell subtraction of Saga minus Worldclim species richness values.

3. Results

3.1. Comparison between both climate models

Spatial correlations between corresponding environmental variables from both climate models yielded extremely high correlation values for temperature variables. The highest correlation values corresponded to the mean temperature during the three hottest months ($r = 0.99$, $p < 0.001$, Table 2), the lowest to the mean temperature during the three coldest months ($r = 0.98$, $p < 0.001$, Table 2). Precipitation variables returned lower but also significant correlations (range 0.46–0.69, Table 2 and Fig. 2). A direct comparison of annual precipitation patterns between both climate models showed that Worldclim provides lower precipitation values than Saga on the humid eastern slopes of the northern Bolivian Andes (map; Fig. 2a). The points above the upper dashed line in the Fig. 2a stem from points placed on this area. The adjacent lowlands of central Bolivia (Chapare; Fig. 1a) are estimated to receive higher precipitation by Worldclim than Saga (dots below the lower dashed line in Fig. 2a).

Worldclim also predicts a fairly uniform precipitation on the east Andean slopes of the northern Bolivian Andes (Fig. 1b), failing

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Table 2
Bivariate correlations between environmental layers from the Saga and Worldclim climate models. Degrees of freedom were corrected according to Dutilleul's criterion.

Environmental variables	*r*	*p*	DF (Dutilleul's corrections)
Annual precipitation	0.57	0.022	6.64
Annual precipitation range	0.46	0.023	5.95
Mean precipitation of the three driest months	0.69	0.021	8.85
Mean precipitation of the three wettest months	0.50	0.027	11.77
Mean annual temperature	0.99	<0.001	4.36
Mean temperature of the three hottest months	0.99	<0.001	4.57
Mean temperature of the three coldest months	0.98	<0.001	4.20

to distinguish the intersecting dry rain-shadow valleys in La Paz and Cochabamba departments. Finally, Worldclim predicts higher rainfall for most of the southern lowlands and Andes, except for extreme south-western Bolivia (Fig. 2a). Although mean annual temperatures from both climate models also reported some spatial differences, these differences were not larger than 4 °C (Fig. 2b).

3.2. Modelling species distributions

Average AUC values obtained for the final distribution maps of bird and fern species were notoriously high using both Saga and Worldclim (>0.84), although values based on Saga were slightly higher (0.94 ± 0.03) than those using Worldclim (0.90 ± 0.03) (Table 1). This difference in favour of Saga was homogeneous for species that are characteristic of humid montane forests, except for the fern *Cyathea squamipes*, which was the only species that showed significantly lower AUC values for Saga than for Worldclim (Table 1). Differences between the models were not as strong for the set of species characteristic of seasonal dry tropical forests. Twenty species did not show significant differences in AUC values (Table 1, $p > 0.05$), for two bird species (*Arremon flavirostris*, *Suiriri suiriri*) Saga values were higher, whereas for four bird species Worldclim values were higher (*Formicivora melanogaster*, *Serpophaga munda*, *Stigmatura budytoides*, *T. harterti*) (Table 1). When comparing the whole subset of species characteristics of this habitat, we did not find significant differences (Table 1).

Variability of AUC values between versions for species characteristic of humid montane forest were quite low, irrespective of which climate model was used (Saga: standard deviation varied from ±0.0001 for *G. erythrotis* to ±0.015 for *Cyathea delgadii*; Worldclim: from ±0.001 for *Delothraupis castaneoventris* to ±0.005 for *Cyathea pungens*). The variability for the subset of species characteristic of seasonally dry tropical forests was somewhat higher but also did not differ between different climate data sets (Saga: from ±0.002 for *Asplenium lorentzii* to ±0.059 for *Asplenium inaequilaterale*; Worldclim: from ±0.001 for *Adiantum rufopunctatum* to ±0.058 for *A. inaequilaterale*; Table 1).

Diversity maps of bird and fern species characteristic of humid montane forests generated by both climate models predicted the species-richest cells on the humid east Andean slopes (Fig. 3a–b and d–e). Worldclim estimations, however, predicted the occurrence of two bird species-rich centres south of the Andean Elbow (up to 11 species) in (1) central Chuquisaca department and (2) at the border between northern Chuquisaca and western Santa Cruz departments (1 and 2; Fig. 3b). Worldclim also predicted the occurrence of three species of tree-ferns (*C. pungens*, *C. multiflora* and *C. delgadii*) in lowlands (3; Fig. 3e). Larger differences resulted when comparing both patterns of species richness on a cell-to-cell basis. Saga predicted higher species richness on the humid east Andean slopes for both taxa than Worldclim (reddish colours; Fig. 3c and f), whereas the latter suggested a higher number of bird species to occur in the cool and dry surroundings of Lake Titicaca (7 species) (4; Figs. 3c and 1a) and the fragmented

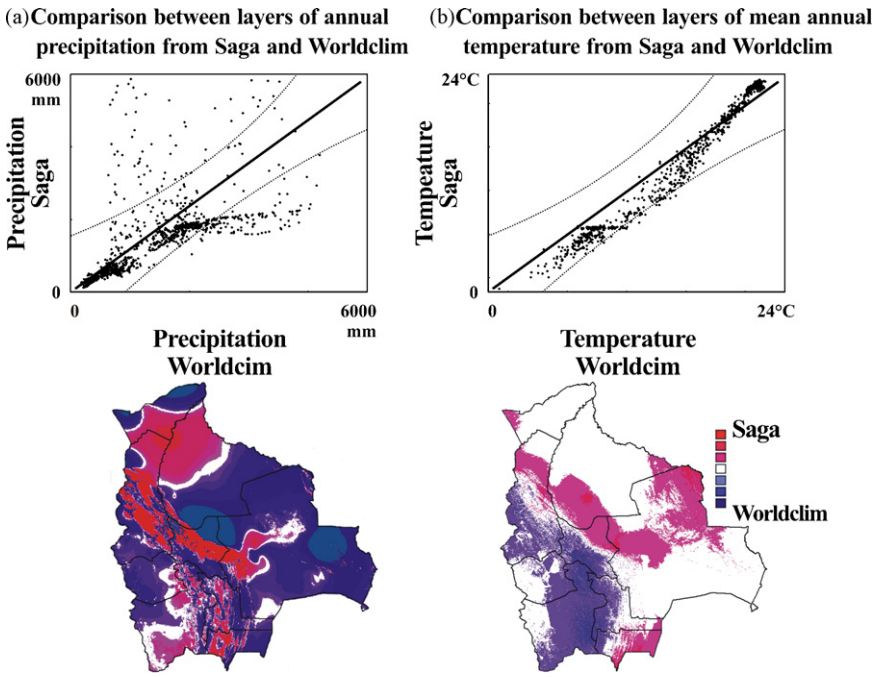

Fig. 2. Graphic correlation between values of mean annual (a) precipitations and (b) temperatures. The *Y*-axis represents values from the Saga model, the *X*-axis Worldclim values. Points above the upper dashed line or below the lower dashed line separate points where the differences between the values from Saga and Worldclim are significant. The maps depict the geographical discordances between both climate models. Reddish tones indicate higher values of Saga in relation to Worldclim, bluish tones the opposite. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of the article.)

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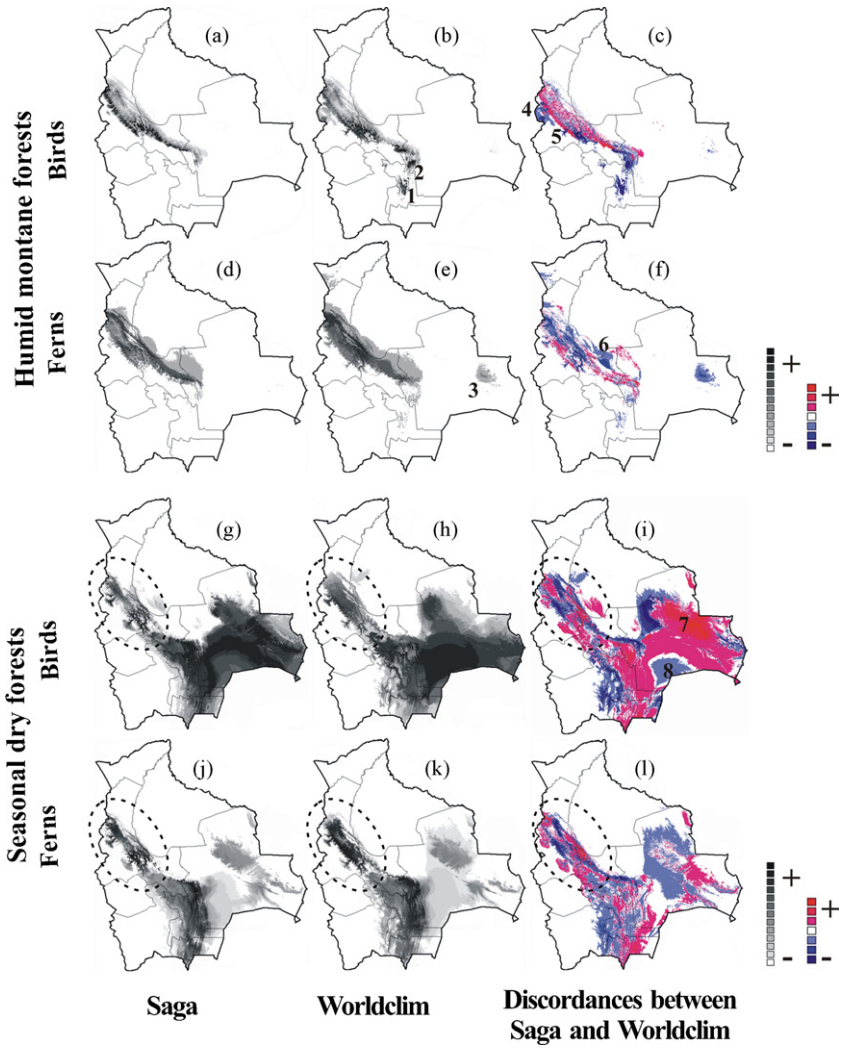

Fig. 3. Patterns of species richness predicted by Maxent models based on climate data from Saga (left) and Worldclim (centre) and tie geographical discordance between the two modelling approaches. Reddish tones indicate higher values based on Saga data in relation to Worldclim data, bluish tones the opposite. The numbers and the circles on the maps are mentioned in the text. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of the article.)

Andean seasonal dry forest (up to 11 species) (5; Figs. 3c and 1a). Importantly, especially for ferns, Worldclim estimated the lowland Chapare region to have higher tree-fern species richness than Saga (6; Fig. 3f).

Despite the lack of statistical differences in AUC values between climate models for species characteristic of seasonal dry forests, the overlapped maps of species richness showed clear differences, not just in the lowlands, but also in the Andes. Models based on Saga calculated cells of higher numbers of co-occurring dry forest bird and fern (dashed circles in Fig. 3g and j, respectively) species in sections of the northern Bolivian Andes (departments of La Paz and Cochabamba) where seasonal dry forests occur as isolated habitat fragments (Fig. 1a). Worldclim, on the other hand, produced a diffuse pattern that was not able to contrast humid from dry habitats in this region of Bolivia (dashed circles; Fig. 3h and k). In other words, models based on Worldclim tended to predict bird and fern species characteristic of dry habitats to occur on the wet Andean slopes north of the Andean Elbow. The dashed circles in Fig. 3i and l show this tendency for both taxa in more detail. Here, the upper humid Andean slopes of the Chapare region were included within the ranges of bird and fern species from dry habitats by models based on Worldclim data. In the dry lowlands, models based on Saga data indicated higher species richness of birds in the central part of the Chiquitano dry forest and in the Cerrado in central Santa Cruz department when compared to models based on Worldclim data (7; Fig. 3i). Models using Worldclim data, on the other hand, predicted higher species richness at the northernmost extreme of the seasonally dry tropical forests and in the Chaco region in southern Santa Cruz (8; Fig. 3i). Model predictions for ferns showed a more complicated spatial pattern in the lowlands. Whereas models based on Worldclim data predicted higher richness in central Santa Cruz, models using Saga data identified the surroundings of the Serranía de Santiago and the Chiquitano dry forest around this area as having more species (Fig. 3l).

The distribution maps of *C. henricae* (the only threatened bird species we worked with) estimated by both climate models show striking differences (Fig. 4). Worldclim estimated a larger distribution, including large areas southern of the Andean Elbow (circle; Fig. 1), as well as portions of Cochabamba valley (1; Fig. 4) and some tracks of humid montane forests (grey circles; Fig. 4).

4. Discussion

4.1. Comparison between both climate models

It is not surprising that temperature layers from both climate models have good spatial concordance. Although slight local deflections due to vertical wind movements caused by difference in

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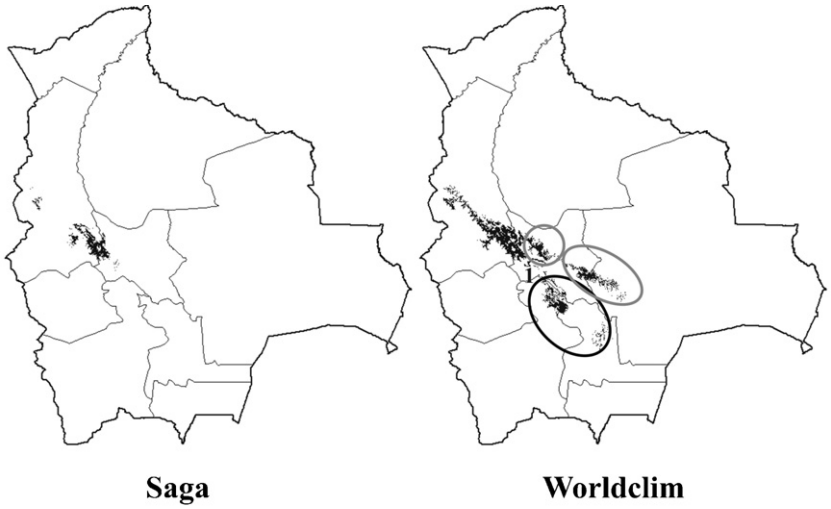

Fig. 4. Distributions of the threatened bird species *Cranioleuca henricae* estimated by Maxent models based on climate data from Saga and Worldclim. Number and circles are mentioned in the text.

air-pressure in mountainous areas may be expected, temperature is strongly negatively correlated with altitude, allowing little room for variation in regional-scale climate models (Killeen et al., 2007). Rainfall patterns, on the other hand, are influenced by a combination of other factors including wind currents, topography, and the diurnal cycle of solar radiation that changes air-pressure, and therefore causes differential precipitations along altitudinal gradients (forcing factors in regional circulation models). Such complex interactions cause a more irregular spatial pattern of rainfall in mountain regions that is not directly correlated to either latitude or altitude.

Unlike Saga, Worldclim does not take into account the effect of topographically influenced regional circulation patterns in estimating the windward and leeward variations of rainfall patterns. We suggest that this methodological difference may be the source of the notable differences in predicted rainfall patterns between both climate models. Killeen et al. (2007) noted that centres of high rainfall predicted by Worldclim along the eastern Andes tend to have an artificial ovoid shape that extends into the more seasonal and drier lowlands. Saga does not depict this pattern. Instead, it mirrors the configuration of the eastern Andean cordillera, and resembles closely the cloud masks presented by Killeen et al. (2007: Fig. 6a–d). Although this may suggest that Saga outperforms Worldclim in predicting rainfall patterns, it must be considered that the masks of cloudiness shown by Killeen et al. (2007) represent the mean pattern of cloudiness at four different times of the day from December to March. Although this period presumably covers most of the rainy season, this figure only offers a qualitative evaluation. A good alternative to evaluate rainfall layers from climate models may be the aggregation of clouds reaching temperatures lower than −65 °C at the top. These clouds are closely related to centres of deep convective rain (Hastenrath, 1997; Killeen et al., 2007). Therefore, a layer that summarizes the frequency of aggregation of clouds with such characteristics may be a reliable independent measure of rainfall. However, the contribution of other sources of precipitation (drizzle, horizontal precipitation, etc.) would still be underestimated.

The accuracy of Worldclim has been assessed in Europe, North America and several tropical regions, all of which have considerably higher densities of climatic field stations than most of the tropical regions in South America, Africa, and Asia (see Fig. 1a–c in Hijmans et al., 2005). Additionally, it is relatively common that field stations in tropical countries have not collected data continuously. This means that although it is possible to find areas with a relatively high density of field stations, not all of them contributed equally with data. Even more importantly, especially in mountainous regions, climate stations tend to be located close to human population centres which are typically found under climatic conditions most suitable to human habitation and agriculture and are rarely representative of the climatic conditions in the entire region. Consequently, estimating rainfall based only on data extracted from field stations may not result in accurate patterns for tropical areas with complex topography and limited numbers field stations.

4.2. Modelling species distributions

Predicted ranges of species characteristic of humid montane forests had a higher model fit when modelled based on Saga. Since the only difference in the modelling process was the use of different climatic models, we can attribute the higher fit of Saga-based models to the climate data. In fact, the patterns of species richness produced by models based on Saga are in closer correspondence to the survey-based knowledge of the distribution of humid montane forests in Bolivia (e.g. Navarro and Maldonado, 2002; Ibisch et al., 2003). Models using Worldclim, on the other hand, predicted the occurrence of several bird and fern species in the surroundings of Lake Titicaca on the Bolivian altiplano, an area without forest cover where the actual climate is much dryer than in the humid montane forests and where none of these species are known to occur (e.g. Hennessey et al., 2003). Importantly, models based on Worldclim also failed to predict the occurrence of some bird species in the humid montane forests of the Chapare region, whereas they wrongly predicted the presence of some humid montane forest species in the Chapare lowlands (ferns; Fig. 3f) and well south of the Andean Elbow (birds; Fig. 3c). Field surveys suggest that the two centres of high bird species richness predicted by models based in Worldclim south of the Andean Elbow (1 and 2; Fig. 3b) are a modelling artefact and that the humid montane forest species modelled here do not occur in these areas (e.g. Hennessey et al., 2003; SKH unpubl.). The Andean Elbow marks the boundary between two distinct ecoregions of montane forest, the tropical humid montane forests of the northern Bolivian Andes (also known as Yungas) and the more seasonal subtropical montane forests (also known as Bolivian-Tucuman forests) south of the Andean Elbow (e.g. Navarro and Maldonado, 2002; Ibisch et al., 2003). Most humid montane forest species reach their southern range limit at the Andean Elbow (e.g. Ridgely and Tudor, 1994; Fjeldså and Mayer, 1996; Hennessey et al., 2003).

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Despite the lack of statistical significance between the AUC values obtained by models based on Worldclim and Saga for seasonal dry forest species ranges, crucial differences emerged between the maps of species richness based on the different climate models. For example, models using Saga more clearly depicted the geographical configuration of the fragments of seasonal dry forests in the northern Bolivian Andes as also indicated by Herzog and Kessler (2002, 2006), Ibisch et al. (2003) and Wood (2006). These outcomes are remarkable since even the predicted ranges using Worlclim obtained values of AUC higher than the commonly indicated minimal acceptable threshold (0.75) (e.g. Fielding and Bell, 1997). If we look at the maps of discrepancies between the patterns of species richness (Fig. 3i and l) further critical differences are evident. Especially remarkable are the marked differences of the estimated ranges of *C. henricae* that obtained the same values of AUC (Table 1). Previous research performed by Maijer and Fjeldså (1997), García-Moreno et al. (1999) and Herzog and Kessler (2002) have shown that this species do not inhabit the Andean seasonally dry forests south of the Cordillera of Cochabamba (1; Fig. 4). The estimated map calculated with Saga is more coherent with the known distribution of its habitat in the Bolivian Andes (Soria-Auza, in prep., SKH unpubl.). This raises the question whether AUC is a suitable index by which to evaluate modelled ranges of species produced by presence-only methods. Although this question is beyond the scope of this study, it is evident that modelled ranges with high AUC values may still be unreliable (see also Lobo et al., 2008; Peterson et al., 2008). This shows the necessity to develop alternative methods to evaluate species distribution modelling techniques that are able to detect fine geographical discrepancies, and not the general of fitness of the models (Araújo and Guisan, 2006). Raes and ter Steege (2007) presented an alternative to evaluate species distribution modelling techniques, but as it is also based on AUC, it still has the same limitations and it is of limited use when the number of species records is the limiting factor. Consequently, ground-truthing of predicted ranges should form an integral part of ecological niche modelling studies, especially if studies are aimed at determining priority areas for conservation action.

Previous studies on the reliability of species distribution models have focused on evaluating the disagreements of predictions produced by different species distribution models (e.g. Elith et al., 2006) or assessed the effect of the spatial data structure (Loiselle et al., 2008), but uncertainties introduced by climate layers have been largely overlooked so far. Our study shows that this uncertainty may have an important impact on the prediction of the distributions of tropical species, where species distribution modelling is increasingly being employed (Hernandez et al., 2008; Hole et al., 2009; Velazques et al. in prep.).

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References

Anderson, R.P., Lew, D., Peterson, A.T., 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol. Model. 162, 211–232.

Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. J. Biogeogr. 33, 1677–1688.

Araújo, M.B., Rahbek, C., 2006. How does climate change affect biodiversity? Science 313, 1396–1397.

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47.

Araújo, M.B., Whittaker, R.J., Ladle, R.J., Erhard, M., 2005. Reducing uncertainty in projections of extinction risk from climate change. Glob. Ecol. Biogeogr. 14, 529–538.

Bahn, V., McGill, B., 2007. Can niche-based distribution models outperform spatial interpolation? Glob. Ecol. Biogeogr. 16, 733–742.

Blanchet, F.G., Legendre, P., Borcard, D., 2009. Forward selection of explanatory variables. Ecology 89, 2623–2632.

Böhner, J., 2005. Advancements and new approaches in climate spatial prediction and environmental modelling. Arbeitsberichte des Geographischen Instituts der HU zu Berlin 109, 49–90.

Canran, L.P., Terence, M.B., Dawson, P.D., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.

Cumming, G.S., 2000. Using habitat models to map diversity: pan-African species richness of ticks (Acari:Ixodida). J. Biogeogr. 27, 425–440.

Dutilleul, P., 1993. Modifying the *t* test for assessing the correlation between two spatial processes. Biometrics 49, 305–314.

Elith, J., Grahan, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachertti-Pereira, R., Schaphire, R.E., Soberon, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.

Fjeldså, J., Mayer, S., 1996. Recent ornithological surveys in the Valles region, southern Bolivia and the possible role of Valles for the evolution of the Andean avifauna. DIVA Technical Report 1. Rønde, Denmark.

García-Moreno, J., Arctander, P., Fjeldså, J., 1999. A case of rapid diversification in the Neotropics: phylogenetic relationships among Cranioleuca spinetails (Aves, Furnaridae). Mol. Phyl. Evol. 12, 273–281.

Graham, K.H., Moritz, C., Williams, S.E., 2006. Habitat history improves prediction of biodiversity in rainforests fauna. PNAS 103, 632–636.

Hastenrath, S., 1997. Annual cycle of upper air circulation and convective activity over tropical Americas. J. Geophys. Res. 102, 4267–4274.

Hennessey, A.B., Herzog, S.K., Sagot, F., 2003. Lista anotada de la saves de Bolivia, 5th edición. Asociación Armonía/BirdLife Internacional, Santa Cruz de la Sierra, Bolivia, 238 pp.

Hernandez, P.A., Franke, I., Herzog, S.K., Pacheco, V., Paniagua, L., Quinana, H.L., Soto, A., Swenson, J.J., Tovar, C., Valqui, T.H., Vargas, J., Young, B.E., 2008. Predicting species distributions in poorly-studied landscapes. Biodivers. Conserv. 17, 1353–1366.

Herzog, S.K., Kessler, M., 2002. Biogeography and composition of dry forests bird communities in Bolivia. J. Ornithol. 143, 171–204.

Herzog, S.K., Kessler, M., 2006. Local *versus* regional control on species richness: a new approach to test for competitive exclusion at the community level. Glob. Ecol. Biogeogr. 15, 163–172.

Herzog, S.K., Soria-Auza, R.W., Hennessey, A.B., 2005. Patrones ecorregionales de riqueza, endemismo y amenaza de la avifauna boliviana: prioridades para la planificación ecorregional. Ecol. Bol. 40, 27–40.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hole, D.G., Willis, S.G., Pain, D.J., Fishpool, L.D., Butchart, H.M., Collingham, Y.C., Rahbek, C., Huntley, B., 2009. Projected impacts of climate change on continental-wide projected area network. Ecol. Lett. 12, 420–431.

Hutchinson, M.F., 1995. Interpolating mean rainfall using thin plate smoothing splines. Int. J. Geogr. Infor. Syst. 9, 385–403.

Ibisch, P.L., Mérida, G., 2003. Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación. Ministerio de desarrollo sostenible - FAN, Santa Cruz de la Sierra, Bolivia, 638 pp.

Ibisch, P.L., Beck, S.G., Gerkmann, B., Carretero, A., 2003. La diversidad Biologica - Ecoregiones y ecosistemas. In: Ibisch, P.L., Merida, G. (Eds.), Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación. Ministerio de desarrollo sostenible - FAN, Santa Cruz de la Sierra, Bolivia, pp. 47–53.

Kessler, M., 2002a. Environmental patterns and ecological correlates of range-size among bromeliad communities of Andean forests in Bolivia. Bot. Rev. 68, 100–127.

Kessler, M., 2002b. Range size and its ecological correlates among the pteridophytes of Carrasco National Park, Bolivia. Glob. Ecol. Biogeogr. 11, 89–102.

Kessler, M., Böhner, J., Kluge, J., 2007. Modelling tree height to assess climatic conditions at tree lines in the Bolivian Andes. Ecol. Model. 207, 223–233.

Killeen, T.J., Douglas, M., Consiglio, T., Jørgenen, P.M., Mejia, J., 2007. Dry spots and wet spots in the Andean hotspot. J. Biogeogr. 34, 1357–1373.

Linares-Palomino, R., Kessler, M., 2009. The role of dispersal ability, climate and spatial separation in shaping biogeographic patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. J. Biogeogr. 36, 280–290.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151.

Loiselle, B.A., Jørgensen, P.M., Consiglio, T., Jiménez, I., Blake, J.G., Lohmann, L.G., Montiel, O.M., 2008. Predicting species distributions from herbarium collec-

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tions: does climate bias in collection sampling influence model outcomes? J. Biogeogr. 35, 105–116.
Luoto, M., Virkkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models depends on spatial resolution. Glob. Ecol. Biogeogr. 16, 34–42.
Maijer, S., Fjeldså, J., 1997. Description of a new Cranioleuca spinetail from Bolivia and a "leapfrog pattern" of geographic variation in the genus. Ibis 139, 606–616.
Navarro, G., Maldonado, M., 2002. Geografía ecológica de Bolivia: Vegetación y ambientes acuáticos. Centro de ecología Simón I. Patiño- Departamento de difusión. Cochabamba, Bolivia.
New, M., Hulme, H., Jones, P., 1999. Representing twentieth-century space-time climate variability. Part I. Development of a 1961–90 mean monthly terrestrial climatology. J. Climate 12, 829–856.
New, M., Lister, D., Hulme, M., Makin, I., 2002. A high resolution data set of surface climate over global land areas. Climate Res. 21, 1–25.
Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34, 102–117.
Peterson, A.T., Papes, M., Soberón, J., 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modelling. Ecol. Model. 213, 63–72.
Phillips, S.T., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling for species geographic distributions. Ecol. Model. 190, 231–259.
Phillips, S.T., Dudík, M., 2008. Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.
Pöyry, J., Luoto, M., Heikkinen, R.K., Saarinen, K., 2008. Species traits are associated whit the quality of bioclimatic models. Glob. Ecol. Biogeogr. 17, 403–414.
Raes, N., ter Steege, H., 2007. A null-model for significance testing of presence-only species distribution models. Ecography 30, 727–736.
Ridgely, R.S., Tudor, G., 1994. The Birds of South America, 2. Oxford University Press, Oxford, UK.
Soria-Auza, R.W., Kessler, M., 2007. Estado del conocimiento y conservación de los helechos y plantas afines en Bolivia. Ecol. Bol. 42, 136–147.
Soria-Auza, R.W., Kessler, M., 2008. The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia. Divers. Distrib. 14, 123–130.
Wood, J.R.I., 2006. Inter-Andean dry forests of Bolivia- Floristic affinities and patterns of endemism: insights from Acanthaceae, Asclepiaceae and Labiateae. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), Neotropical Savannas and Seasonally Dry Forests. Press Boca Raton, FL, USA, pp. 235–256.